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Colour Vision: Colouring the Dark

Dispatch

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Humans lose colour vision at night and it has often been assumed that this happens to other animals as well. It is not true of nocturnal moths, however: a recent study has shown that the elephant hawk moth makes use of trichromatic colour vision when seeking flowers by starlight.

Our inability to see colour at night does not seem to be a puzzle. For one thing, colour vision requires signals from cone photoreceptors which, compared to the rods, are insensitive to dim light. But more fundamentally, photon noise makes colour signals unreliable at low intensities. A photoreceptor is essentially a device for counting photons, and colour vision is based on differences in photon counts by receptors that differ in spectral sensitivity. The count from a fixed light source fluctuates with Poisson statistics — the variance is equal to the mean — and at low intensities this unavoidable source of noise limits visual discrimination. Achromatic intensity is given by the mean of one noisy signal, but chromatic signals are given by the difference between the means, and the noise by the sum of the variances. We might therefore predict that colour vision fails around dusk because of poor signal-to-noise ratio. Given this fundamental limitation it is not surprising that nocturnal mammals, such as the owl monkey *Aotus*, often have only one type of cone and are probably colour-blind [1]. A nocturnal habit is often thought to have led to ancestral placental mammals losing two of the four cone types believed to have been present in their vertebrate ancestors [2].

Perhaps because photon noise is unavoidable — and in any case it seems unreasonable for other species to enjoy colour at night when we cannot — there have been few studies of colour vision by nocturnal animals. But now Kelber *et al.* [3] have reported that a strictly nocturnal insect, the elephant hawkmoth (*Deilephila elpenor*), sees colour at starlight intensities, prompting a closer look at the limitations on, and uses of, colour vision. This new study used a procedure originated ninety years ago, in a classic demonstration of colour vision by von Frisch [4], who showed that honeybees learn to distinguish a blue or yellow food dish from any shade of grey. Kelber *et al.* [3] found that moths could do this task, but they were unable to learn the brightness of the feeders. By comparison humans set the same task could distinguish stimuli only by their brightness, and so were colour blind. Why, then, do moths retain colour vision at low intensities? Part of the answer lies in the very high photon flux provided by the moth's eye.

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Sensitivity and Moth Eye Optics

The enhanced sensitivity of the eyes of moths lies in the optical system of their eyes. Insect eyes fall into two broad optical types: apposition and superposition, a distinction first made explicit by Sigmund Exner [5], in his famous monograph originally published in 1891. In apposition eyes (Figure 1), each receptive structure — a rhabdom, consisting of the photopigment-bearing microvilli of, typically, eight receptor cells — has its own lens, which forms a small inverted image at the distal tip of the rhabdom. Each rhabdom is thus illuminated by a single lens, the diameter of which is commonly about 25 μm. Superposition eyes are superficially very similar in appearance, but the crucial difference is that many facets contribute to a single erect image on the receptor layer (Figure 1), which is correspondingly brighter than the multiple images in an apposition eye. Kelber *et al.* [3] estimate that, in the eye of *Deilephila*, 568 facets contribute light to each point on the image. Apposition eyes are typical of diurnal insects such as bees, grasshoppers and dragonflies, and superposition eyes are mainly found in insects active at twilight or later into the night, such as moths and fireflies.

The optical arrangement that allows superposition images to be formed is unconventional. As Exner [5] was able to show, the structures involved are not simple lenses but behave optically as two-lens telescopes. They act — as in astronomical telescopes — as inverters, and thereby provide a ray-path that redirects the entering rays back across the axis of each element. As Figure 1 shows, this allows ray-bundles from a large segment of the eye to come to a single focus, after traveling across the eye's 'clear zone', a feature not present in apposition eyes. Exner also showed that each optical element has insufficient surface curvature to provide the ray-bending required for it to act as a telescope, and he came up with a novel solution: a 'lens cylinder' in which each element has a gradient of refractive index, falling from center to periphery. Ray-bending occurs continuously within such a structure, rather than just at the curved interfaces, providing ray-paths that are the equivalent of the lens-based telescopes.

How do the sensitivities of apposition and superposition eyes compare? For a given environmental luminance, the amount of light that enters a photoreceptor, independent of the type of eye involved, is proportional to the area of the aperture of the imaging system multiplied by $\Delta\rho^2$, where $\Delta\rho$ is the receptor's acceptance angle [6]. This is the angle in outside space over which a receptor receives light. For *Deilephila* the aperture area is $n\pi D^2/4$, where the facet diameter D is 29 μm, and n is the number of contributing facets. This comes to 375,175 μm^2. For the apposition eye of a worker bee (*Apis*), a diurnal forager, the aperture diameter of a single facet is 25 μm and the area 491 μm^2. The ratio of aperture areas for moth and bee is thus 764:1. The receptor acceptance angles ($\Delta\rho$) are not very different from each other: 3° for *Deilephila* [3] and

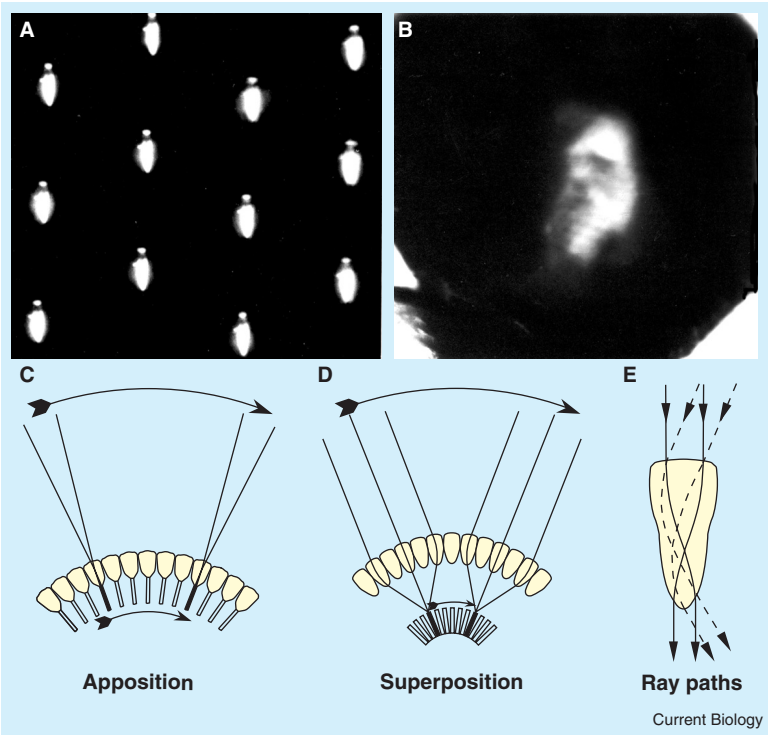

Figure 1.

(A) Inverted images of a candle flame in the eye of a robber fly, which has apposition optics. (B) Single erect image of Darwin photographed in the superposition eye of a firefly. (C) Image formation in an apposition eye; the overall image is erect. (D) Image formation in a superposition eye. (E) Ray paths of axial and eccentric beams through one of the telescopic optical elements in a superposition eye. (Adapted from [6].)

2.6° for *Apis* [7]. This slightly increases the ratio of light entering the receptors by $(3/2.6)^2$ to 1017:1.

Thus, from the same background moth receptors obtain three orders of magnitude more light than bee receptors. This is roughly the difference between bright sunlight and roomlight, or between full moonlight and unobscured starlight. Put another way, it buys about one hour of extra foraging after the sun has set. But *Deilephila* continues to be active much further into the night than this, and the optical advantage of the superposition eye, already impressive, must be extended by other mechanisms, as Kelber *et al.* [3] point out.

An improved photon count for the neurons supplying visual information to the brain could be obtained by combining the outputs of many receptors (as occurs in humans). This, however, decreases resolution — by effectively increasing the acceptance angle $\Delta\rho$ — and as moths still have to fly and find flowers, the use of this strategy is limited. The alternative is to increase the sampling time of the receptors, perhaps from tens to hundreds of milliseconds. Again this is a limited strategy for a flying insect. Nevertheless, between them these two forms of summation — spatial and temporal — probably provide another two orders of magnitude of sensitivity, which is just about enough to bridge the remaining gap between dusk and starlight.

The Uses of Colour Vision

So far we have discussed limitations to colour vision imposed by photon noise, but to understand the differences between humans and moths it may also be helpful to consider the uses of colour vision. Colours can be distinguished both by their achromatic intensity (or 'brightness'), and their chromaticity ('hue' and 'saturation'). At the lowest intensity tested by Kelber *et al.* [3], humans could distinguish test stimuli only by their brightness, and so were colour-blind. The moths were strikingly different, they could see colour — they could distinguish a spectral colour from any shade of grey — but they were unable to learn brightness.

Why should moths disregard brightness when human rely on it? In fact, the moth's behaviour is not entirely surprising, because in many behavioural contexts other animals are similar. When required to discriminate a spectral light from its background, many animals, including honeybees, birds and humans in bright light, are more sensitive to differences in chromaticity than in achromatic intensity [8–12] (Figure 2). As illumination falls, however, humans begin to differ from moths. First, we become relatively more sensitive to achromatic brightness differences derived from cone outputs; later, cone responses fail and we use rod vision (Figure 2).

This tendency to use chromatic and disregard achromatic information cannot be understood purely in terms of the signal-to-noise ratio in photoreceptors. In particular, when the task is to locate or identity objects, variations in illumination caused by shadowing may be a serious problem. Under these circumstances, achromatic information about object colours is likely to be more seriously affected that chromatic information. Unfortunately, compared to photon noise in receptors, it is difficult to specify the magnitude of this 'ecological noise'. Consequently it is not easy to predict the behavioural tasks and range of light intensities where colour vision is useful for a given species.

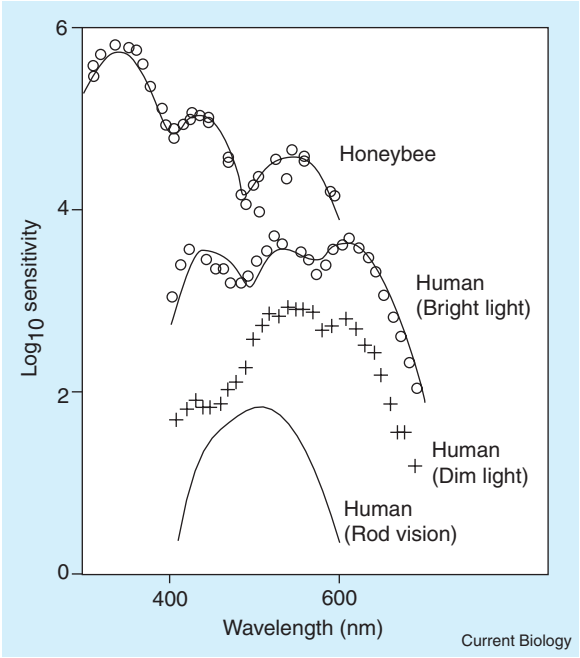

Figure 2. Spectral sensitivities of humans [13,14] and honeybees [8] given by the reciprocal relative photon flux of a given wavelength required to produce a detectable stimulus over an adapting background.

Symbols show experimental data, and the fitted curves in the upper two plots are predictions of a model which assumes that discrimination is based on responses of colour-opponent mechanisms, without any achromatic input [11]. This model does not predict colour thresholds for humans in dim light probably because we combine chromatic and luminance signals. The human data for bright and dim light correspond to adapting intensities of approximately 3,000 cd m^{-2} and 5 cd m^{-2}, respectively. The curve for rod vision is the human scotopic spectral sensitivity [14]. Curves are displaced vertically for clarity.

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